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INTRODUCTION

The study of seed dispersal between the widely separated forest patches (forest islands) of the eastern Great Plains can contribute to understanding effects of deforestation in the more complex forest island landscapes of the eastern United States. In the East, there is growing concern that the dissection of regional forests and the creation of small forest islands surrounded by non-forest uses (e.g., agriculture) may be affecting plant species richness and developmental patterns of vegetation (Levenson 1976), as has already been noted in the tropics (Gomez-Pompa et al. 1972). Curtis (1956) showed that the presettlement forest area in a portion of Green County, Wisconsin had been reduced by 70% as of 1882, 90% by 1902, 95% by 1935, and more than 96% by 1950.

The effect of distance in altering seed exchange between forest islands has not been directly tested. However, the use of forest islands as study sites has provided some clues about the effects of distance (isolation) on dispersal and forest composition. Scanlan (1975), Tramer and Suhrweir (1975), and Levenson (1976) all noted that the species richness of forest stands in Minnesota, Ohio, and Wisconsin, respectively, was inversely proportional to the degree of isolation from neighboring stands. It is not clearly understood whether the characteristics of deforested landscapes preferentially reduce the abundance of species with certain dispersal characteristics (e.g., heavy animal-dispersed and heavy wind-dispersed seeds).

Planted forest stands in the prairie-forest border offer a desirable set of conditions for studying the effect of landscape pattern on propagule dispersal. The islands are generally small (ca. 0.1-25 hectares) and species-poor, so that tree surveys can be conducted rapidly. Also, the closest possible origin of observed reproduction in each island can be easily determined even if the closest seed source is a different island. In addition, a wide range of inter-island distances occur in these landscapes.

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The study of selected tree claims, shelterbelts, and natural ravine forests in southeastern South Dakota was undertaken during the summer of 1976 to examine the distances propagules were carried by wind and animals between forest islands. The similarities in tree species of the study area with Ohio and Wisconsin (Table 1) make the South Dakota forest islands even more pertinent for study, since seed dispersal information on these species would be useful in determining forest dynamics in other areas where they occur.

Table 1. The list of species studied in the South Dakota islands occurring naturally in other forest island landscapes of the Midwest according to Kingsley and Mayer (1970) and Spencer and Thorne (1972). Dispersal of the listed tree species would be more difficult to study in Ohio and Wisconsin where many are more ubiquitous.

Tree Species	Location and Occurrence in forest islands		
	Study area	Ohio	Wisconsin
Acer negundo L. (boxelder)	common	common	common
Acer saccharinum L. (silver maple)	common	common	common
Catalpa speciosa Warder (n. catalpa)	common	rare	rare
Celtis occidentalis L. (hackberry)	common	common	common
Elaeagnus angustifolia L. (Russian olive)	common	rare	rare
Fraxinus pennsylvanica Marsh. (gr. ash)	common	common	common
Juglans nigra L. (black walnut)	common	common	common
Juniperus virginiana L. (e. red cedar)	common	uncommon	common
Morus rubra L. (red mulberry)	common	common	common
Populus deltoides Bartr. (e. cottonwood)	common	common	common
Prunus serotina Ehrh. (black cherry)	uncommon	common	common
Quercus macrocarpa Michx. (bur oak)	common	common	common
Ulmus americana L. (American elm)	common	common	common
Ulmus pumila L. (Siberian elm)	common	rare	rare

STUDY AREAS

The study areas are located near Newton Hills State Park (Lincoln County) and Turkey Ridge (Turner County), 40 and 70 kilometers south and southwest of Sioux Falls, South Dakota, respectively (Fig. 1). This region was predominantly tall grass prairie prior to settlement, although forest vegetation occurred along streams, rivers, and upland ravines where moisture, microclimate, soils, and limited fires permitted their natural establishment. Early settlers were able to claim land by planting trees under the Timber Culture Act of 1873. Now many of these square- or rectangular-shaped tree claims are nearly 100 years old and provide protection for farm homes and buildings. During the 1930's severe drought conditions and soil loss due to winds stimulated soil and crop protection measures, leading to the 1935 Great Plains Shelterbelt Project. Contrary to the

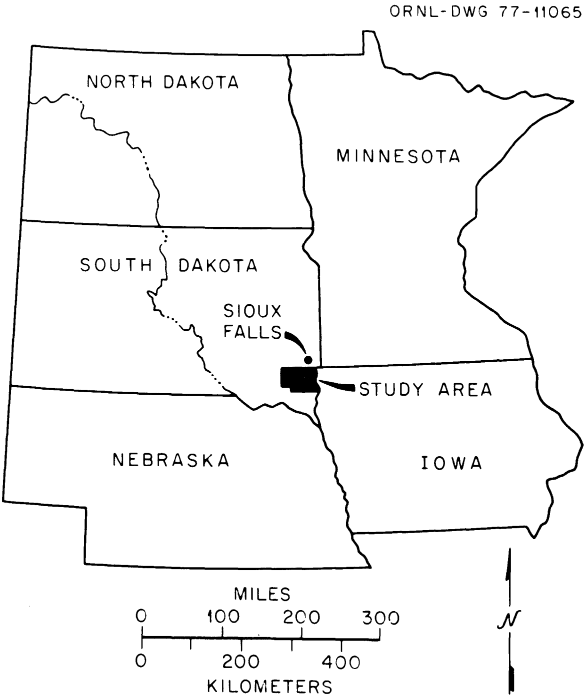

Figure 1. Study area location.

block-type shape of the tree claims, shelterbelts are usually no more than 5 to 13 rows of trees wide (20 meters) but may be over a kilometer in length. Most plantings are quite isolated with intervening distances ranging from a few hundred meters to well over a kilometer. Current aerial photographs (1970) show that the forest vegetation in these two study areas consists of natural hardwood forests confined to lowland or rough upland areas, tree claims about 2 to 3 per section (260 hectares), and shelterbelts (less than one per section).

Originally, settlers obtained most planting stock from nearby lowland sites. Therefore, the initial composition of the tree claims was usually a subset of those species available from naturally occurring stands. Later, some locally exotic species were planted as well (e.g., black walnut, northern catalpa). By far, the most frequently occurring species are boxelder, green ash, American elm, Siberian elm, and hackberry (Table 1). Other species include catalpa, eastern cottonwood, Russian olive, bur oak, black walnut, silver maple, eastern red cedar, and black cherry.

Among the minor species, Russian olive, eastern cottonwood, and northern catalpa produced no seedlings in the plantings. Silver maple produced few seedlings despite ample seed supply, and black walnut, eastern red cedar, black cherry, and bur oak germinated almost as well as the major species. The relative and absolute germination success of species or the effects of browsing on seedling mortality were not investigated in detail.

METHODS

A reconnaissance of tree seedlings and saplings in selected forest islands was made and compared to the arboreal layer (surviving trees of species planted originally). If seedlings and saplings occurred in the understory but not in the tree layer, it was assumed that they originated from a different island. Absence of seedlings and seed trees of species with relatively high germination probabilities (ash, boxelder, oak, elm, hackberry, walnut, cedar, and cherry) was assumed to be due to an extremely limited seed rain. Where invading tree species were found, nearby islands were checked for possible source trees and the nearest source was recorded.

Forest islands were initially selected using recent (ca. 1970) black-and-white aerial photographs provided by the Soil Conservation Service. All tracts selected were 0.1-1.25 kilometers from naturally occurring oak forests (Fig. 2). Many of the stands were eliminated from consideration after field investigations showed that they had been grazed within the past few years or had an otherwise visibly disturbed understory. Seven forest islands were investigated in detail in the Newton Hills Region, while four islands were examined in the vicinity of Turkey Ridge. All stands were located on well-drained upland locations with slopes of less than three percent.

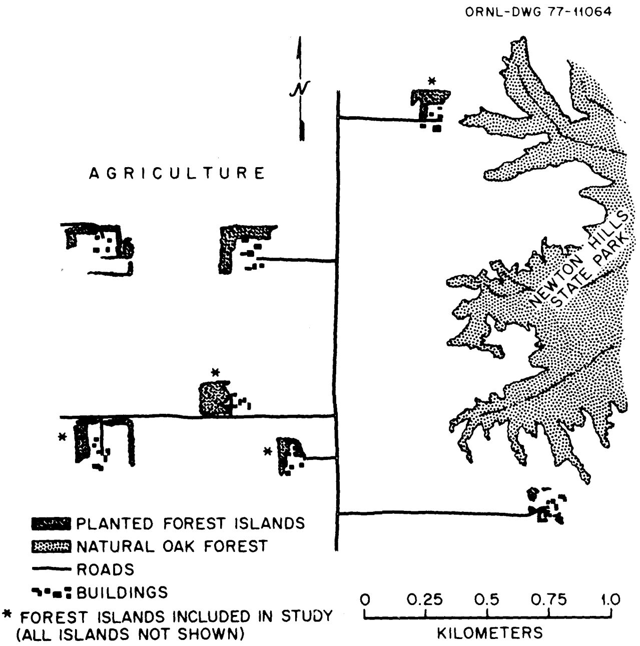

Figure 2. Redrawn from aerial photographs, this portion of the study area containing a part of Newton Hills State Park shows the distribution of forested islands. The ravines in the Park contain naturally occurring oak forests. Other forests have been planted up to 100 years ago under the Timber Culture Act of 1873 or as shelterbelts.

RESULTS

Newton Hills

The naturally-occurring bur oak forests in the ravines of Newton Hills State Park are conspicuous either from aerial photographs or ground observation. No seed-bearing oak trees occurred in any of the nearby plantings. However, naturally established seedlings (1-5 years old) were found in two of the plantings. In one case, the closest source trees were located 100 meters away, and in the other about 500 meters from the progeny. The other sites investigated, which ranged from 500-1,250 meters from an acorn source, had no oak progeny (Table 2).

Major long-distance acorn dispersers in the area are the blue jay and the fox squirrel. Fox squirrels inhabit the island areas, brushy areas between islands, and natural forests. Blue jays are common breeding birds in this region.

Two islands had boxelder wind-dispersed progeny but no seed-bearing boxelder trees, and the distances to the nearest sources were nearly the same as reported for oaks, 100 meters and 425 meters. However, the number of boxelder saplings in the more distant stand was considerably higher than the number of oak seedlings (25 vs. 4) suggesting that invasion by boxelder was greater than by oak, assuming equal mortality and viability. Interestingly, 90% of the boxelder progeny in the distant stand occurred in the edge of the island facing (nearest to) the suspected source. The effect of prevailing winds on ingrowth of plantings on windward aspects was not investigated.

Several short-distance observations were also made for some additional species. Hackberry and ash seedlings were found 100 meters from the nearest source and mulberry, which is easily dispersed by a multitude of animals, was about 150 meters from the nearest source. Although black walnut trees were frequently encountered in the plantings, no walnut seedlings were found in stands without seed trees.

Our observations of plantings ranging up to 100 years of age indicate that ingrowth to the stand (between rows of trees) does not usually occur until the planting is quite old (50 to 75 years) and a well-buffered microclimate is established. Hence, there is high mortality in the seedling and sapling layer. Because of this, only the oldest plantings contain a historical record of seed rain as interpreted from the structure and composition of ingrowth trees.

Turkey Ridge

In the vicinity of Turkey Ridge, only the island closest to an acorn source (325 meters) had oak seedlings in the understory (Table 2). This island was comprised of two blocks of forest joined by a small connector several tree rows wide. Again, as mentioned earlier for the Newton Hills site, the seedlings were located on the source-facing side of the stand, indicating that the dispersal vector released or buried the seeds near the first point of contact with forest vegetation. Also, the oak seedlings occurred in the block of forest connected to the source area by a small, natural drainage ravine which was vegetated with trees and thick herbaceous vegetation but no oak species. The adjacent block had no natural con-

Table 2. Survey of forest islands lacking oak species in the canopy

Dominant tree species	Size (hectares)	Oak seedlings or saplings present	Nearest oak source (meters)
Ash-Maple	0.19	yes	140
Mixed*	0.45	no	200
Mixed*	0.65	yes	325
Elm	0.26	no	400
Elm-Ash	0.29	yes	500
Mixed*	1.07	no	730
Boxelder	0.31	no	750
Mixed*	1.30	no	830
Ash-Elm-Boxelder	0.81	no	930
Mixed*	0.16	no	940
Hackberry-Ash-Elm	0.61	no	1250

*"Mixed" refers to stands having more than three dominant species.

nector and no oak seedlings even though the distance to the source was the same as for the connected block. Admittedly, the sample size is small but this observation lends strength to a hypothesis (Diamond 1975) that such vegetation corridors can serve as conduits of seed dispersal for selected species.

DISCUSSION

The limited data collected support the hypothesis that the effective dispersal distances of certain arboreal propagules can be estimated in southeastern South Dakota using the suggested techniques. If more data collection supports this view, the application of island biogeographical concepts to forest island landscapes (Sullivan and Shaffer 1975, Diamond 1975), similar to the one in southeastern South Dakota, will be more readily testable.

The inter-island dispersal of heavy, animal-dispersed propagules such as acorns (Table 2) was effective up to about 500 meters between the forest islands of the study area. Similar dispersal limits were determined from somewhat lighter propagules such as boxelder, hackberry, ash, and mulberry although this second group of propagules appeared to be dispersed in greater numbers. It is not known if the food preferences (McAtee 1947, Smith and Follmer 1972) of animal vectors affect quantitative dispersal of propagules within the distance limits identified.

Assuming that dispersal vectors (e.g., wind speed, presence of certain animal species) are similar for the same trees in other landscapes, small forest islands separated by more than 500 meters of non-forested land may experience a long-term decline in the abundance of these species. For example, if some islands of oak in such a landscape were eliminated by disturbance, there would be little or no invasion of oak propagules from outside stands because of distance barriers. Thus, the oaks would either not become established or would be much less important than previously due to a reduced number of oak seedlings available to eventually compete for canopy space.

Because squirrels are the only likely dispersers of black walnut in the region, and this is the animal-dispersed species observed to be the most confined to propagule-source islands, we doubt that squirrels carry propagules from source islands in order to scatter-hoard them in distant non-source islands. Rather, they may actively travel between islands but store propagules near the source for later use. Because acorns may be dispersed by both blue jays and squirrels, we expect them to be carried greater distances from source areas than walnuts. This was suggested from limited field observations.

The observed tendency for both wind- and animal-dispersed seeds to come to rest or be buried on the source-facing side of the islands suggests that ingrowth to an island is spatially uneven and that seed source location and strength could be inferred for some species by a spatial analysis of composition and structure of forest islands. Uncultivated connectors among islands, although observed in only one case, may channel and encourage inter-island propagule dispersal by mammals (i.e., squirrels) and alter ingrowth dynamics for arboreal species.

There are many factors believed to affect the dispersal and survival of propagules between forest islands which were not investigated such as (1) the "attractiveness" of forest islands to faunal vectors, (2) the size of the islands, (3) forest island density requirements of animal vectors and their mobility limitations, (4) habitat modifications through time and space caused by forest development which affects propagule germination and survival, (5) faunal vector food preferences, and (6) unusual climatic events.

The observations of this study are of sufficient interest that more comprehensive studies are suggested for the region. The information gained from such research can help man understand the effects of deforestation in eastern landscapes and how this might affect the natural distribution of tree species and their importance in forest systems. It is felt that a similar study of natural understory species (*Zanthoxylum americanum, Prunus virginiana*) can provide important additional information for understanding and constructing processes of seed dispersal and forest development.

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